DISTURBANCE AND COMMUNITY DYNAMICS ON HEUWELTJIES

BOTANY ECOLOGY HONOURS PROJECT
1990
SUPERVISOR: DR W.J.BOND

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ABSTRACT

The vegetation and floristic structure of Mima-like mounds (heuweltjies) was studied at Tierberg (Great Karoo) and at Worcester (Succulent Karoo). Disturbance intensity on mounds was independently assessed and related to the vegetation ocurring on each mound. On-mound exclosures were built, and granivory experiments were conducted both on- and off-mound. Distinct successional stages in the vegetation could be correlated with different levels of disturbance intensity. The presence of this disturbance driven succession on-mound contrasts with the prevailing view of solely event driven arid-land dynamics, which does not allow for succession. *Pteronia incana* is an indicator of low disturbance mounds, while *Psilocaulon utile* is an indicator of high disturbance mounds at Worcester. *Rhus/Euclea* patches are the successional climax state. Favoured regeneration sites for the key species at Worcester were quantified. A competitive hierarchy for the key on-mound species at Worcester is proposed, and the competitive abilities of the species are discussed. Grazing of on-mound annuals by micromammals may have a major structuring role in community dynamics. Granivory on-mound is intense, but is insignificant off-mound. The possible processes behind these patterns are discussed and the significance of these findings is reviewed.

INTRODUCTION

Mima-like earth mounds, commonly known as "heuweltjies", are widespread in the renosterveld and Karroid areas of the western Cape region of South Africa (Lovegrove and Siegfried 1986). These circular mounds are usually less than 1m high and about 10-20m in diameter (pers.obs.). The on-mound soils have higher clay and silt fractions, water status, pH, and macro- and microelemental concentrations than the soils between mounds (Midgley and Musil 1990). The vegetation on mounds is noticeably different from the vegetation between mounds, with many different species and a much greater density and size of plants on-mound (Knight *et al* 1989; Milton *et al* -In press; pers.obs.). Most research has concentrated on identifying the mechanisms of mound formation, the most popular hypotheses invoking the effects of termite and molerat burrowing (Lovegrove and Siegfried 1986; 1989). A recent study suggests that a wide variety of other animals may be involved in the generation and formation of these mounds (Dean and Milton -In press). These other animals include the aardvark *Orycteropus afer*, various lizards, buck, mongooses, snakes, felids, scorpions, beetles and rodents, as well as ostrich and porcupine. There is thus a wide range of animals which may disturb both the soil and the vegetation on these mounds.

There are no published studies of competitive interactions between on-mound plants, or on the influence of herbivory and granivory by rodents on the dynamics of these plants. This study is thus an attempt to describe the differences in vegetation among mounds, with a view to relating this to different levels of disturbance by animals. Knight *et al* (1989) found that only 18,7% of plant species were shared between mounds in the Clanwilliam district (Dry mountain fynbos - Karoo interface), and they suggested that this low value may be due to non-uniform disturbance regimes imposed by termites, molerats and aardvarks. What this implies is that the different species have different habitat disturbance requirements, but the authors did not hint at any sequential species replacement *i.e.* successional stages. Mentis *et al* (1989) feel that most semi-arid communities cannot be

understood in terms of conventional successional theory as they are usually event driven systems and succession is often on too great a time scale for us to detect. In this study I hope to examine this phenomenon and describe and quantify any successional species replacements that may be evident. A positive result would support Knight *et al's* (1989) contention that non-uniform disturbance on mounds promotes floristic variation.

The potential impact of rodents as both herbivores and granivores was investigated, as their activities may be an important component of the disturbance regime affecting the floristic composition on mounds.

This study is not an attempt to determine the reasons behind the different vegetation structure and species composition between on- and off-mound areas, but is rather an attempt at describing the patterns and suggesting possible processes that produce the among mound floristic/structural differences.

METHODS

A) Study areas

The study was undertaken at two very different sites. Experimental and observational studies were carried out in the Worcester Veld Reserve from July to September 1990, while observational records were made at Tierberg Karoo research site near Prince Albert between March and July 1990.

The Tierberg site is approximately 25km east of Prince Albert and is therefore on the southern edge of the Great Karoo, a semi-arid region. Annual rainfall is approximately 167mm (92 year average). The biotic and abiotic features of the study site are discussed in depth by Milton *et al* (In press). Sheep have been excluded from the study site since 1987.

The Department of Agriculture's Worcester Veld Reserve lies some 140km NE of Cape Town (33°38'S 19°27'E) at an altitude of 300-450m, along the southern foothills of the Hex River mountains. Climate is typically Mediterranean, with most of the annual 250mm falling in winter. Soils are weakly developed, generally shallow (less than 0,5m), and are derived mainly from Witteberg and Bokkeveld series shales (Theron 1983). The vegetation of this area, included within the Succulent Karoo Biome (Rutherford and Westfall 1986), is dominated by chamaephytes, many of which are succulent. As might be expected from the higher rainfall figures, the Worcester vegetation is significantly denser and more speciose than the Tierberg vegetation (pers.obs.). Most of the sampling was carried out on the top of the low hills so that steep gradients were not a complicating factor. Domestic stock have not grazed the area for at least 30 years (M.B.Bayer -pers.comm.).

B) Assessment of disturbance intensity

i) Tierberg

Brant's whistling rats (*Parotomys brantsii*) form extensive burrow systems in approximately 30% of the Tierberg heuweltjies (Milton *et al* -In press). These rats are herbivorous, succulents making up more than 50% of their diet, and the rodents are found in densities of two to six rats per occupied heuweltjie (Du Plessis 1989). Their burrow systems have an average area of 7X7m, with an average of 46 burrow entrances per heuweltjie (Du Plessis 1989). Collections of harvested plant material are frequently deposited at the entrance to active burrows (See Plate 1a; pers.obs.), so that the number of active rats on the heuweltjies can be estimated by counting these dumps. In addition, non-active burrow entrances were counted on each heuweltjie to give an indication of past and present rodent use intensity. Certain mounds contain only numerous unnocupied burrows and these mounds were classed as disturbed, but abandoned.

Various other animals disturb the heuweltjies, the most important being aardvark *Orycteropus afer* and steenbok *Raphicerus campestris* (Milton *et al* -In press). The former dig vigorously on many mounds, while the latter use these disturbances as midden sites. The number of visible scratchings and middens was recorded to give a further indication of disturbance intensity. Three different levels of disturbance could ultimately be recognized, *viz.* high, medium and low.

ii) Worcester

The major disturbance on the lower hillslopes at Worcester appears to be the burrowing activities of the molerat *Cryptomys hottentottus*. However, on the upper plateau (where the study site was located) molerat activity seems to be minimal, with most of the disturbance being due to mice, termites and buck.

Grysbok (*Raphicerus melanotis*) have been recorded on the mounds, where they lie under the dense vegetation during the day (pers.obs.), while klipspringer (*Oreotragus oreotragus*) have been seen in the rocky areas adjacent to the study site. The middens on the heuweltjies are believed to be largely the result of grysbok territorial activity. The number of middens on each mound was recorded.

Termite (*Microhodotermes viator*) frass is often very common on the mounds. The quantity was estimated and this was used together with observations of the number of active termite ground holes to approximate the intensity of termite induced disturbance.

Various species of rodent are likely to be present on the mounds, although only the granivorous striped mouse (*Rhabdomys pumilio*) was actually seen in the area. Nests of the herbivorous bush-karoo rat (*Otomys unisulcatus*) were rare on the mounds, but their presence indicates the occurrence of this species. The density of cleared rodent "runways" was used as a guide to the intensity of rodent activity on the mounds. Mounds were ultimately divided into two disturbance categories : high and low.

C) Line transects

In order to see whether different mound disturbance regimes could be correlated with a particular vegetation type, the floristic and vegetational structure of high and low disturbance mounds was compared, using data collected by the line intercept method.

A tape was stretched the diameter of the mound and the vegetation changes below the tape were recorded. The tape was placed along a representative area of the mound and was positioned so as to include as much of the variation as possible. Eight low disturbance mounds and five high disturbance mounds were investigated at Worcester. At Tierberg it was possible to split the mounds up into three levels of disturbance intensity, so that nine highly disturbed mounds, ten mounds of medium disturbance intensity, and ten mounds of low disturbance intensity were surveyed. The measured distance (*i.e.*mound diameter) varied between 8 and 25m.

In order to assess whether a single transect adequately expressed the floristic composition on the mound three transects were made on two test mounds. The combined result for three transects on each mound was then compared with the result from the initial transect on the mound and these were found to be essentially the same, indicating that a single transect would adequately represent the vegetational and floristic structure of the mounds. All species below the tape were recorded, as was open space and all dead plants. These measurements were then represented as a percentage of the total diameter measured . For example, if the diameter was 15,0m and 3,0m of *Euphorbia mauritanica* was recorded, this species would represent 20% of the total mound space. The species listed in Table 1 made up about 90% of the mound flora at Tierberg, so that it was not difficult to select key species.

D) Plant species interactions and regeneration sites

In this section of the study I asked the following questions : 1) Do the key species (as identified by the line intercept method) display preferred regeneration sites? 2) Are some species better able to overgrow/outcompete others? If so, can the species be arranged in a dominance/successional hierarchy?

This study was conducted at Worcester only. Seven important/dominant elements of the mound flora were selected using data from the line transects, *viz.* open space, *Psilocaulon utile*, *Ruschia caroli*, *Euphorbia burmanii*, *E.mauritanica*, *Pteronia incana* and *Euclea undulata/Rhus incisa*. These species were selected as they are consistently the most common species on the mounds (except where *P.utile* was absent), and they determine the vegetation structure of the mounds. *Rhus* and *Euclea* make up one distinct group, as they occupy the same structural niche and the presence of either one or the other seems to be random.

Regeneration sites for these six species were then noted by recording the location of young plants. Young plants were identified by their small size and stem diameters, and by their lack of woodiness. These plants were usually larger than seedlings, being anywhere between 5 and 25cm tall, depending on the species. Young plants grow either in open space or under the canopies of adult plants. The identity of all adult "nurse" plants was recorded.

Adult interactions were assessed by making approximately 20 random observations of each key species on the mounds. Two different mounds were examined so that there is an average of 40 observations for each species. In each case the possible competitive interactions were examined by assessing which species was overgrowing another. Young plants were avoided, as these were included in the previous study. An adult plant was recorded as being overgrown by another if more than 50% of its canopy and stem area was covered (shaded)by the other plant. If both plants appeared to be overgrowing each other by 50%

each was scored as overgrowing the other, which would effectively show that the species were competitive equals. Very often species A would oust species B from an area by growing towards it and forcing species B to grow away at an extreme angle, in which case species A was recorded as overgrowing species B. The number of times that one species overgrew another was represented as a percentage of the total observations for the successful species.

E) Exclosures

The hypothesis that small mammal herbivory has an effect on on-mound community structure was tested by building exclosure plots. Four experimental exclosures were built on the mounds, each with a control. Two were situated on heavily disturbed mounds and two on lightly disturbed mounds. Each experiment consisted of a 1X1m wire mesh (1,4cm diameter holes) exclosure, with the bottom of the wire buried in the ground to discourage rodents from digging underneath. The sides were 1m in height and supported by fence droppers on each corner, while the top was uncovered so as to alter the environment as little as possible. The adjacent control was of an identical construction except that the bottom 10cm of wire was rolled up to allow free access to small terrestrial animals. Each exclosure unit was situated in a relatively open space within the mound and an attempt was made to include similar vegetation in both experimental and control plots, although this was not always possible. Two snap-traps were set in each experimental exclosure to ensure that mice did not eat the plants within.

A single young plant of *Euphorbia mauritanica* seedling was transplanted into both the control and the experimental exclosures on one of the highly disturbed mounds, in order to test for herbivory. Similar *E.mauritanica* plants were transplanted into control and experimental exclosures on a lightly disturbed mound.

The exclosures were monitored five times over the period July - September 1990, and each time any changes in vegetation composition were noted.

F) Granivory experiment

Five Petri dishes were placed in both covered or open sites on-mound, while another five were positioned ~~on~~ off-mound. This was repeated on four mounds, two being highly disturbed and the other two being densely vegetated. Two sunflower seeds and approximately 2ml of budgie seed were placed in each Petri dish. This experiment was set out in the afternoon of the 24 September 1990 and was collected two days later.

G) Statistics

Fisher's exact test was used to test for significance in the results of the granivory experiment, while a discriminant analysis and Mann Whitney two-tailed test was used in the analysis of mound species composition. A discriminant analysis allows the identification of the species that are most useful in differentiating between high and low disturbance mound floras, and can tell us whether the disturbed and undisturbed mound floras are distinct from each other as a whole.

RESULTS

A) Tierberg

Assessment of on-mound disturbance intensity, independent of vegetational and floristic structure, was relatively easy due to the sparse vegetation and consequent visibility of any mammalian disturbances.

Mounds with a low level of disturbance are dominated by *Malephora lutea*, with a mean cover of 29% (Table1). More *M. lutea* grows on low disturbance mounds than on either high or medium disturbance mounds . This trend is also visible in the figures for dead plants of this species.

Psilocaulon utile is found most commonly on mounds of medium disturbance intensity and is rarest on lightly disturbed mounds, while dead plants are most common on heavily disturbed mounds. *Pteronia pallens* is equally common on lightly and heavily disturbed mounds, but is twice as common on mounds of medium disturbance intensity. *Augea capensis* is equally common on all mounds. The amount of open space on the mounds is similar for both low and medium disturbance mounds and is a little greater on heavily disturbed mounds. This trend is repeated by the figures for mean mound diameter.

Table 1 Disturbance intensity and mound species composition at Tierberg. Figures represent standard deviations and mean percentage cover for each mound type.

Species	Mound disturbance intensity					
	Low (n=10)		Medium (n=10)		High (n=9)	
	Mean %	S.D.	Mean %	S.D.	Mean %	S.D.
Open space	32,6	12,7	35,4	9,4	41,3	15,8
Malephora lutea	29,3	8.7	15,7	5,4	13,7	9,8
Dead *M.lutea*	8,3	5,5	3,7	3,1	4,8	4,1
Psilocaulon utile	13,2	12,3	22,2	11,4	16,1	11,8
Dead *P.utile*	1,2	1,9	1,5	2,2	3,3	5,3
Pteronia pallens	3,9	2,4	7,9	4,8	4,2	2,3
Augea capensis	4,5	3,2	3,3	5,9	4,3	5,5
Dead *A.capensis*	0,9	1,5	1,3	3,4	1,2	2,6

B) Worcester

i) Line transect data

Vegetation on mounds at Worcester is more than twice as dense as the vegetation on Tierberg mounds (Worcester mounds have less than half the amount of open space that Tierberg mounds have - Table 2a). These two are not the same thing.

Highly disturbed mounds did not differ significantly from mounds of low disturbance in the quantity of open space recorded (p=0.7). *Pteronia incana* was the dominant species on lightly disturbed mounds, but lost this position to *Euphorbia burmanii* on heavily disturbed

Ruschia caroli from Table 2

mounds. *P.incana* is significantly more common on lightly disturbed mounds ($p=0.07$). Although there is a lot of variation among the mounds, more dead *E.mauritanica* were found on highly disturbed mounds and this trend seems to hold true for dead plants of *E.burmanii* as well.

Stands of *Rhus/Euclea* are equally common on mounds of high and low intensity disturbance, but the abundance variability is great. The only two species to show an increase in cover on heavily disturbed mounds were *Psilocaulon utile* and *E.burmanii*. *P.utile* is absent from all lightly disturbed mounds and the large standard deviation for this species on highly disturbed mounds indicates that its abundance is very variable.

Ruschia caroli is common on both mound categories, but is more common in lightly disturbed areas, where it is the second most abundant species.

Table 2a Disturbance and species composition on mounds at Worcester. Figures refer to standard deviations and mean cover percentages for each mound category.

Species	Mound disturbance intensity				
	Low (n=8)		High (n=5)		
	Mean %	S.D.	Mean %	S.D.	Mann Whitney
Open space	14,7	4,5	15,0	8,8	p=0.7
Ruschia caroli	16,5	8,0	16,0	13,2	p=0.7
Dead *R.caroli*	1,1	2,1	2,2	3,0	p=0.7
Psilocaulon utile	0	0	9,4	10,5	p<0.01 *
Euphorbia mauritanica	11,3	11,4	9,4	3,7	p=0.7
Dead *E.mauritanica*	0,6	1,7	2,6	5,8	p=0.7
E.burmanii	10,2	4,0	13,4	9,4	p=0.7
Dead *E.burmanii*	0,0	0,0	1,2	2,7	p=0.2
Rhus spp./Euclea undulata	7,0	10,7	2,2	4,9	p=0.2
Pteronia incana	21,8	10,6	10,2	5,1	p=0.07 *
Mean mound diameter (m)	16,4	2,8	18,9	4,4	

Table 2b Unstandardized discriminant function coefficients for the key species at Worcester.

Species	Coefficient
Open space	-0.03569
Ruschia caroli	-0.01208
Dead *R.caroli*	-0.41328
Euphorbia mauritanica	-0.16497
Dead *E.mauritanica*	0.27966
E.burmanii	0.04981
Dead *E.burmanii*	1.24809
Psilocaulon utile	0.16667
Rhus/Euclea	-0.14122
Constant	6.20115

ii) Regeneration sites and plant species interactions

a) Regeneration sites

Ruschia caroli forms dense mats and this appears to be a favoured regeneration site for *Euphorbia burmanii*, *E.mauritanica* and *Pteronia incana* (Table 3). Open space is colonised by all the key species, although this is not a site exploited to any great degree by *E.mauritanica*, which has more young plants under *Rhus/Euclea* and *Pteronia incana*. The best space colonisers are the mat-forming species *R.caroli* and *Psilocaulon utile*. These species produce numerous lateral branches which are capable of forming adventitious roots, thus alleviating the need to produce small, vulnerable seedlings, very few of which were found on the mounds. Although mats of *R.caroli* appear to be a favoured regeneration site, this is not the case for *P.utile*. This is surprising as both have similar growth forms.

The only species with young plants of its own species under its canopy was the *Rhus/Euclea* group, and this can be attributed to the fact that these young plants were root sprouts rather than true seedlings. This species group produced large numbers of these sprouts from vigorous lateral branches, but no true seedlings were seen. *Pteronia incana* is

Table 3 The location of young plants of the key species at Worcester. Figures represent the percentage of records for each seedling species.

Young plant species	Nurse species							
	Rhus/Euclea	*E.burm.*	*E.maur.*	*P.incana*	*P.utile*	*R.caroli*	Space	n
Rhus/Euclea rootsprouts	50	0	0	0	0	0	50	20
Euphorbia burmanii	24	0	3	10	1	31	31	20
E.mauritanica	17	0	3	24	7	34	14	40
Pteronia incana	0	0	18	0	0	45	36	20
Ruschia caroli	These species reproduce largely vegetatively, the stems producing							
Psilocaulon utile	adventitious roots. Very few seedlings.							

Table 4 Who overgrows who ? The number of times that one species overgrows another (as a percentage of the interactions of the canopy species).

Canopy species	Sub-canopy species						
	P.utile	*R.caroli*	*E.burm.*	*E.maur.*	*Pt.incana.*	*Rhus*	n=
Psil.utile	NA	10	0	0	0	0	60
R.caroli	10	NA	0	0	0	0	60
E.burmanii	35	44	NA	0	16	2	35
E.mauritanica	20	21	36	NA	21	5	60
Pter.incana	9	53	32	14	NA	0	50
Rhus/Euclea	25	17	34	10	13	NA	35

also able to produce adventitious roots and this may help explain its presence under the short lived *E.mauritanica*.

No young plants of any species were recorded under adults of the short-lived *E.burmanii*.

b) Adult interactions

This section is concerned entirely with adult plant interactions. There may have been a slight error involved in sampling as a small plant living beneath the canopy of another may not necessarily be a seedling - it may merely be stunted as a result of competition. An, older stunted plant can usually be told from a seedling by the woody, thicker stems and harder nodes, but this distinction can not always be made and some stunted plants may have been called seedlings and vice versa.

However, some interesting trends were revealed. A striking feature of Table 4 is the paucity of positive records for the upper half of the Table. This suggests a well defined species hierarchy - interactions between the key species are not equal or random.

Psilocaulon utile and *Ruschia caroli* seldom overgrow each other, but when they do it is normally in equal proportions *i.e.* one species does not dominate the other. What often happens is that both species tend to die back at the point at which the interaction took place. These two mat-forming species are low down in the dominance hierarchy and are not able to overgrow any other species to any significant degree, while they are overgrown by all the other species.

Euphorbia burmanii is unable to overgrow *E.mauritanica*, although the latter frequently overgrows the former. *E.burmanii* occassionally

overgrows *Pteronia incana*, although this interaction usually results in the latter dominating the former. When *E.mauritanica* interacts with *P.incana* the situation is usually reversed as the former is able to outgrow the latter and shade it. *Rhus/Euclea* is clearly the stable state which is not prone to invasion. None of the key species are successfully able to overgrow *Rhus/Euclea* , although the latter species frequently send out shoots which overgrow the other species. *E.mauritanica* and *P.incana* seem less susceptible to overgrowth by *Rhus/Euclea* than do the other key species, perhaps due to their ability to grow upwards into a gap very quickly.

iii) Exclosures

None of the transplanted young *Euphorbia mauritanica* plants were eaten, neither in the excloures nor in the controls.

The controls indicated that herbivory on annual plants is a potentially important factor in mound dynamics (Figure 1). Three of the four exclosures (Figures 1a,1c, and 1d) had severely eaten annuals in the controls, while the annuals in the corresponding experiments increased their cover abundance with time (Plate 2f). These annuals were starting to set seed by Week 8 and therefore cover was starting to drop dramatically as the plants withered. Species eaten include *Oxalis* spp., *Pentzia* sp., *Oncosiphon pilulifera*, *Lepidium africanum* and *Troglophyton parvulum*. Young root sprouts of *Euclea undulata* had

Figure 1 The resuts of the experimental exclosures built on-mound at Worcester. The data refer only to the annual plant component as the perennial species did not have enough time to respond to the new conditions. Control plots allowed free access to rodents. Sites 1 and 2 were situated on heavily disturbed mounds, while Sites 3 and 4 were situated on lightly disturbed mounds. The general trend is for annual species cover to increase in experimental exclosures and to remain stable or decrease in control plots.

Figure 1a: Site 1

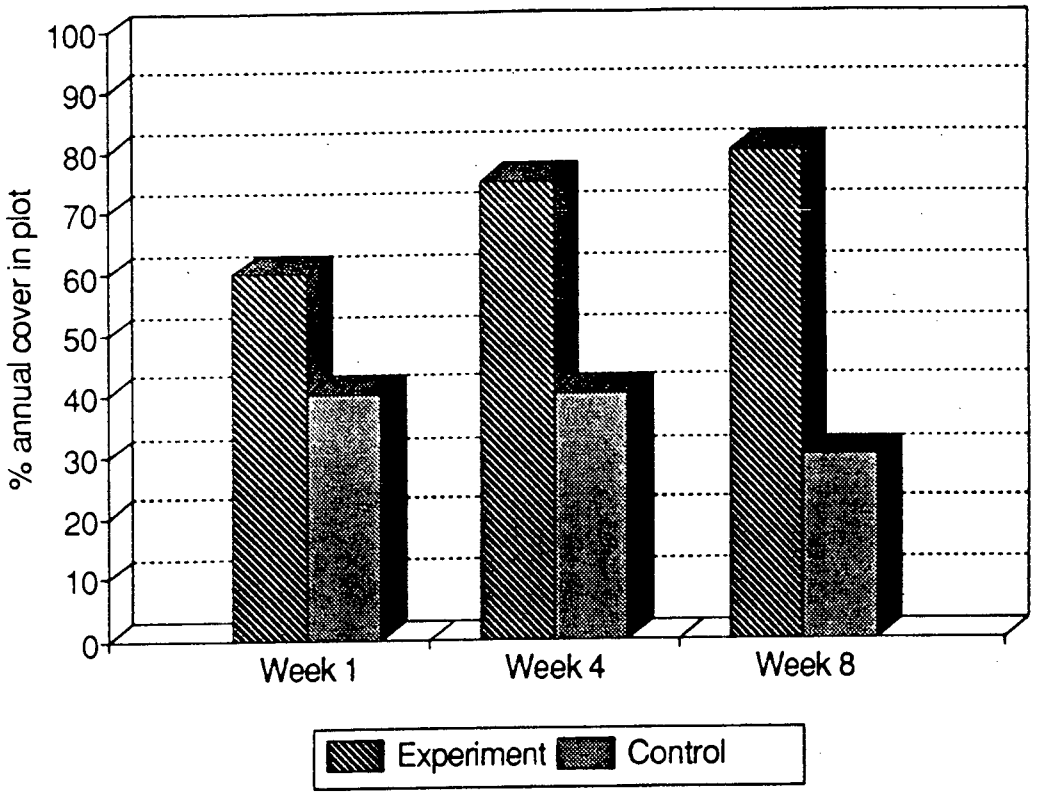


Figure 1b: Site 2

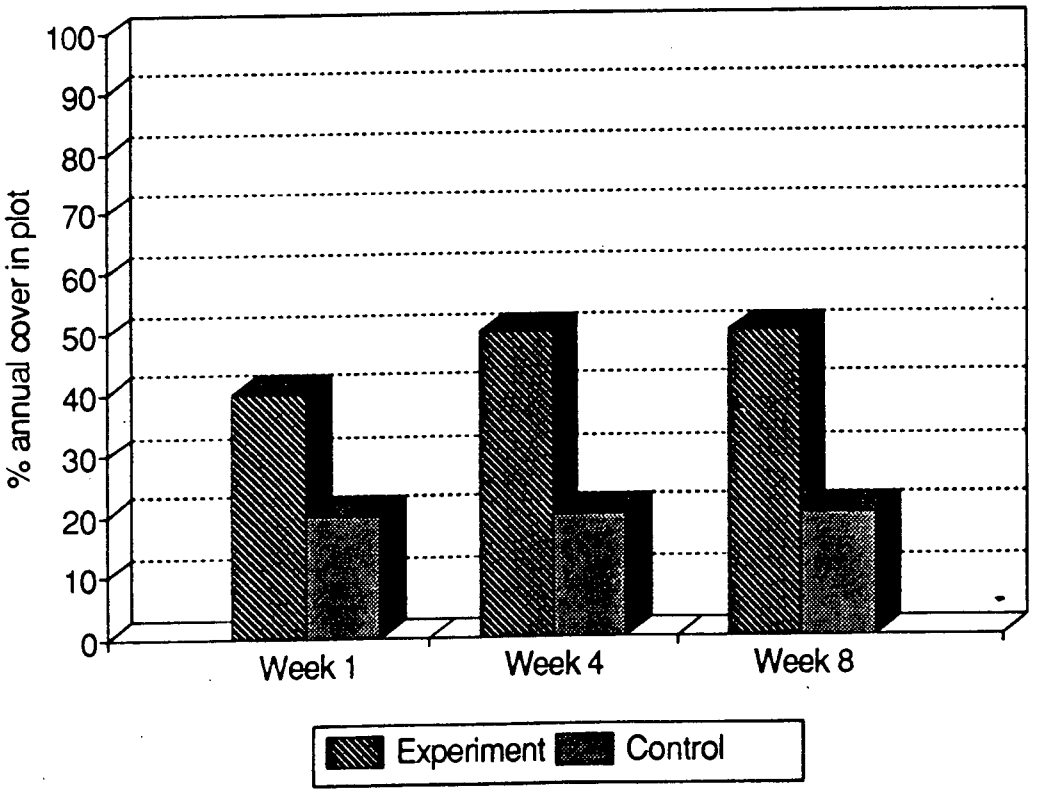


Figure 1c: Site 3

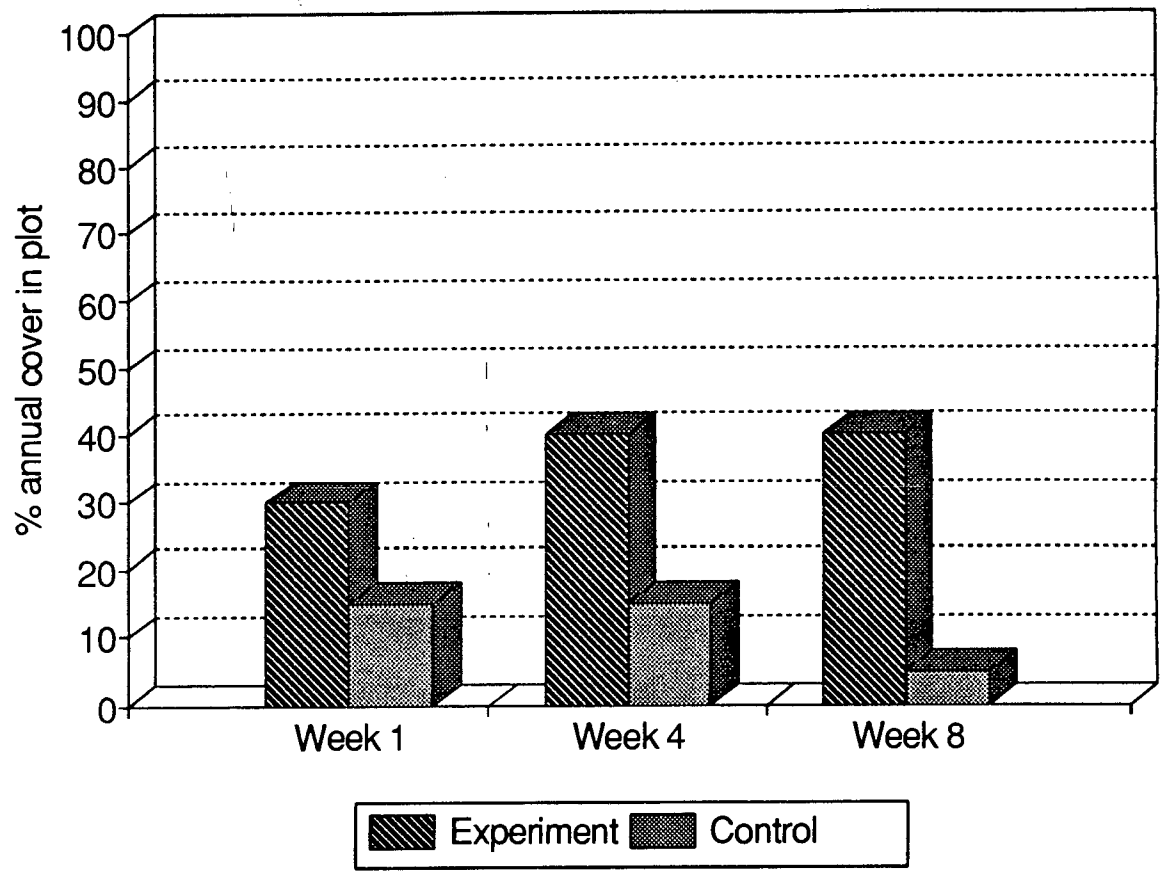
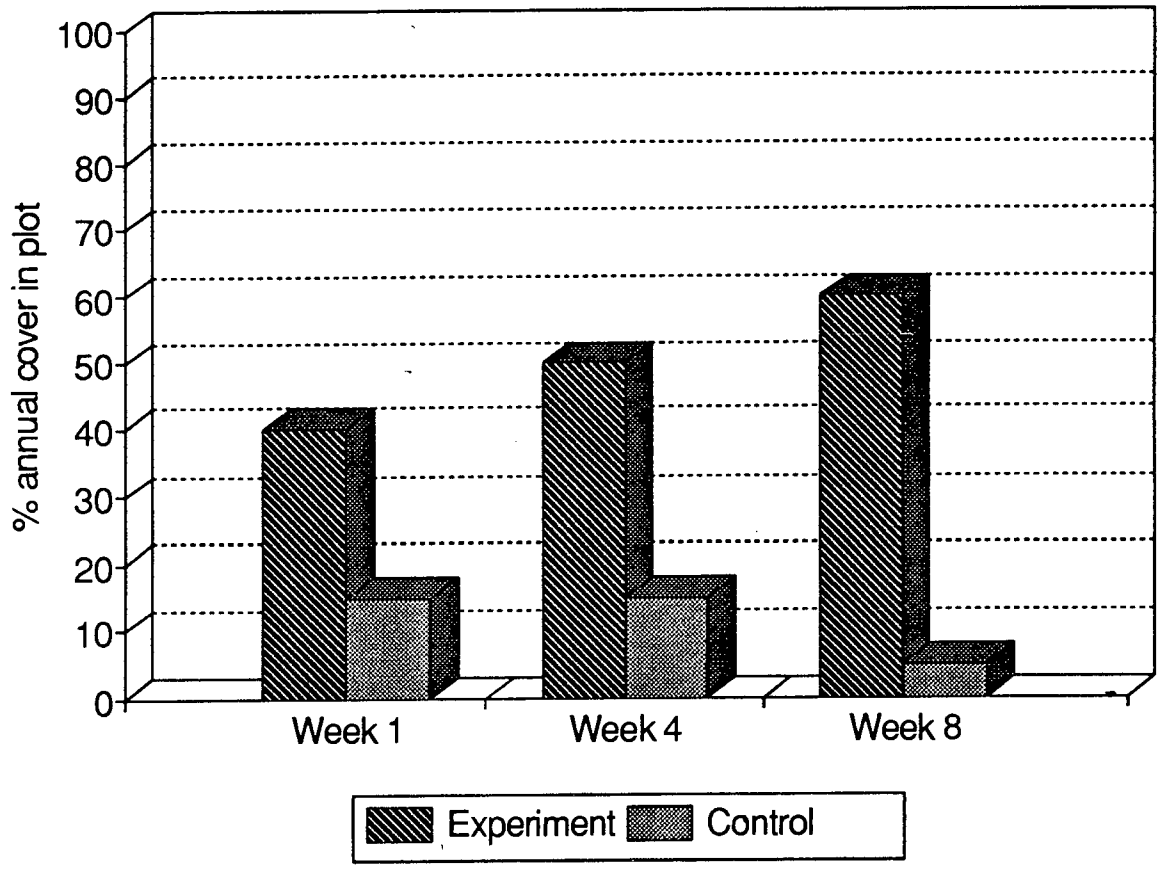


Figure 1d: Site 4



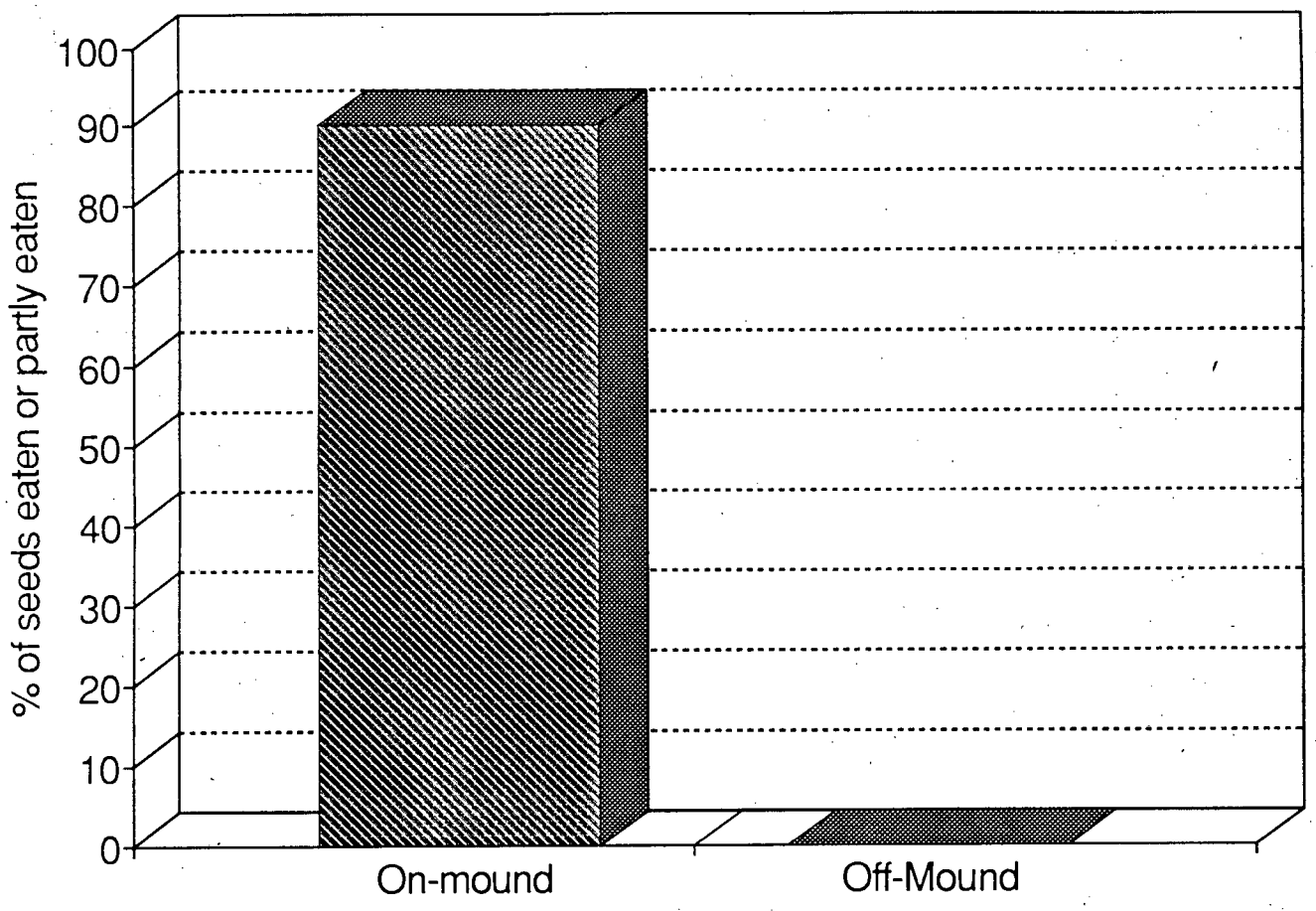
their terminal buds removed by herbivores. Annuals displayed the most striking response to exclosure, the time scale perhaps being too short for any major changes in the perennial species.

iv) Granivory experiment

No seeds were eaten in any of the 20 Petri dishes placed off-mound, while 15 of the 20 Petri dishes on-mound had all seeds husked or removed. This difference is highly significant ($p<0,01$). The remainder of on-mound Petri dishes had only some of the seeds eaten, and two dishes contained all the original seeds (*i.e.* uneaten). Of the remainder, one had a single sunflower seed eaten , another had all the budgie seed removed but neither of the sunflower seeds, and the third dish had both sunflower and some of the budgie seed removed (Figure 2).

There was no significant difference ($p=0,5$) in seed removal between high and low disturbance mounds.

Figure 2 The combined results for four cafeteria experiments conducted both on- and off-mound at Worcester. 20 food were dishes placed on-mound and 20 food dishes were placed off-mound. Each dish contained two sunflower seeds and about half a teaspoon of commercial budgie seed.



DISCUSSION

Non-uniform disturbance regimes on-mound appear to promote floristic variation at both Worcester and Tierberg. At both sites species can be identified which display increased abundance on heavily disturbed mounds, and other species which display decreased abundance on such mounds. The independent assessment of mound disturbance intensity was supported by data reflecting associated changes in floristic and vegetational structure. Isn't this a circular argument?

In addition, there are a number of broadly tolerant species which show no abundance shifts in accordance with changing disturbance intensity. The two study sites will be discussed separately due to their different floras.

A) Tierberg

Malephora lutea is sensitive to severe disturbance and is largely replaced by *Psilocaulon utile* on heavily disturbed mounds. The latter

species is able to thrive in areas with numerous old or active burrows (Plates 1a and 1d), while the former favours abandoned or undisturbed mounds (Plates 1b and 1c). This could possibly be attributed to the herbivorous activities of *Parotomys brantsii*, which eats large quantities of *M.lutea* (pers.obs.). The whistling rat may effectively denude a mound of *M.lutea* by the combined effects of its burrowing and preferential feeding, leaving the (seemingly) less palatable, hardier, *P.utile* to dominate the mound (Plate 1d). There is some evidence for *P.utile* being more common on mounds of intermediate disturbance intensity (Table1), which suggests that excessive rodent burrowing may reduce even the number of *P.utile* (note the increased numbers of dead *P.utile* on heavily disturbed mounds). This is supported by observation and Table 1, heavily disturbed mounds having more open space than mounds with intermediate levels of disturbance. This extra space may have been left by the greater numbers of dead *P.utile* plants on heavily disturbed mounds (Table 1).

Pteronia pallens is the dominant plant between mounds (Milton *et al* - In press; pers.obs.), but is also found on-mound, where it is most common on mounds of intermediate disturbance intensity (Plates 1b, 1c and 1d). Why this should be is unknown, but this result should be interpreted with caution as the standard deviation on mounds of intermediate disturbance intensity is high, suggesting that chance stochastic events have played a role in the establishment of the species. Mentis *et al* (1989) have emphasised that many arid and semi-arid communities are event driven and need an event to overcome the inertia within the system. These events are stochastic and many species have been shown to have population dynamics closely associated with this stochasticity.

Plate 1a Tierberg - High intensity disturbance mound. Note the *Parotomys* burrows and dumps of harvested *Malephora lutea* at the entrance to an occupied burrow. *Psilocaulon utile* dominates the centre of the mound, while *M.lutea* is confined to the edge (right of picture).

Plate 1b Tierberg - Low intensity disturbance mound. The bright green bush is *Pteronia pallens*, which dominates the intermound areas (middle distance). Low disturbance (no *Parotomys* burrows or aardvark scratchings visible) means that *M.lutea* dominates the mound, and *P.pallens* is able to invade the mound. *Psilocaulon utile* is absent.

Plate 1c Tierberg - Medium intensity disturbance mound. Abandoned *Parotomys* burrows are visible near the white stake and *M. lutea* dominates the sparse vegetation. *Pteronia pallens* (dark green) has begun to invade this old mound which is not subject to any form of disturbance at present.

Plate 1d Tierberg - Medium intensity disturbance mound. *Parotomys* is presently active on this mound which may account for the dominance of *Psilocaulon utile* and the absence of *M. lutea*. *Pteronia pallens* is rare on the mound. The light-green succulent is *Augea capensis*.

B) **Worcester**

Splitting the mounds into two categories at Worcester was often difficult as most of the mounds contained numerous rodent "runways", although the vegetation is very different on some mounds. This discrepancy between disturbance intensity classification and vegetation structure may have been partly due to the high density of *Rhabdomys pumilio* runways on-mound (pers.obs.). These mice are granivorous and do not play a major role in the defoliation/killing of live plants. The canonical correlation of 0.96864 supports the *a posteriori* classification of mounds into high and low disturbnce categories based on vegetation and floristic structure. Mounds were grouped *a priori* into high and low disturbance categories using only features independent of vegetation structure. What this high correlation means is that vegetation can be used effectively as an indicator of mound disturbance intensity. Some noteworthy trends are evident.

Some sort of disturbance is necessary for the establishment of *Psilocaulon utile* on mounds, as it is entirely absent from mounds with a very low disturbance intensity. Dense populations of this species are found on some of the heavily disturbed mounds (Plate 2a), although the species was absent from other heavily disturbed mounds nearby (note large standard deviation). This su ggests that the species may not always be able to reach a newly disturbed site. If this happens, *Ruschia caroli* may quickly occupy the open, disturbed space and come to dominate the mound in the place of *P.utile.* These two species may thus be viewed as competitive equivalents in many cases. The discriminant analysis revealed that *P.utile* was the species that best distinguished heavily disturbed mounds (correlation coeff.=0.6374; p=0.02). None of the other species showed significant positive associations with heavily disturbed mounds.

McAuliffe (1988) studied a simple Arizona desert community and found that two main species were present. *Ambrosia* recruits mostly in open spaces (85%), while *Larrea* always recruits under *Ambrosia*. *Ambrosia*

Plate 2a Worcester - Heavy disturbance. Dense mats of *Psilocaulon utile* are covering any available space, with a few *Euphorbia burmanii* (left centre) and *E.mauritanica* (right centre and background) growing up through the mats and overgrowing the space-coloniser.

Plate 2b Worcester - Low disturbance. Large, dry specimens of *E.mauritanica* lie near the spaces that their deaths have left. This space is being colonised by *P.utile* (arrowed) and by the annual component (light brown). The large grey bush on the left is *Pteronia incana.* The presence of this species indicates a lightly disturbed mound. Dense *E.burmanii* and *E.mauritanica* are visible in the middle distance.

Plate 2c Worcester - Low disturbance. *Ruschia caroli* invading open space and beginning to form dense mats. Young *Pteronia incana* plants (grey) are regenerating in open space and within *R.caroli* mats.

Plates 2d Worcester - Low disturbance. *Pteronia incana* (grey), *E.burmanii* (centre) and *E.mauritanica* (right and centre middle) are nearly competitive equals, although *E.mauritanica* tends to overgrow the other two species.

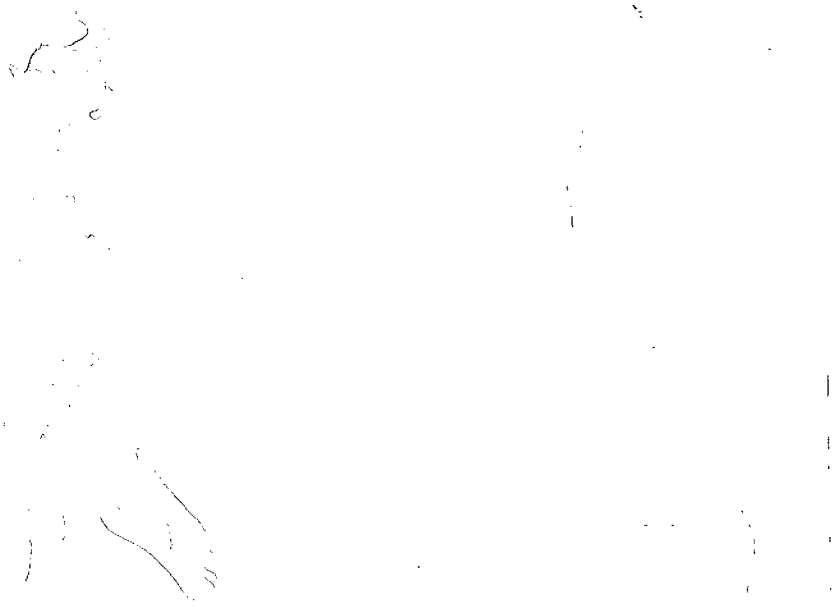


Plate 2e Worcester - Low disturbance. Large plant of *E.mauritanica* (left) competing with a *Rhus* sp.(right). The *Rhus* has a slight height advantage and is able to overgrow the *Euphorbia*. Both species cease growth along most of the contact zone.

Plate 2f Worcester - Exclosure plot on heavily disturbed mound 8 weeks after being constructed. Note the reduced annual component in the control plot on the right. Most of the annuals are *Pentzia* sp. and *Oxalis* sp.

is thus the space-coloniser in this example and is functionally equivalent to *Ruschia caroli* and *Psilocaulon utile* at Worcester. The results of the present study suggest that *E.burmanii*, *E.mauritanica* and *Pteronia incana* are all analogous to *Larrea* in their recruitment strategy, as they favour the sub-canopy of the space-colonising species (*R.caroli*). This interstudy comparison suggests that there are common patterns of recruitment in the world's arid and semi-arid regions.

Euphorbia mauritanica grows more abundantly in lightly disturbed mounds and appears to suffer increased mortality when exposed to increased disturbance levels. Seedling transplant experiments suffered from insufficient replicates, but preliminary results suggest that *E.mauritanica* seedlings are not readily eliminated by herbivory. The reduced numbers of *E.mauritanica* and *Pteronia incana* plants on heavily disturbed mounds (cf. Plates 2a and 2b) is not likely to be due to increased seed predation (granivory) in these ares, as the cafetaria experiments showed no difference between high and low disturbance mounds. It is thus difficult to say exactly what is causing the drop in numbers on heavily disturbed mounds. *E.mauritanica* is short-lived and leaves large open spaces when it dies (pers.obs.), and this is probably on e of the major methods of gap creation in lightly disturbed mounds (Plate 2b).

E.burmanii is more common on heavily disturbed mounds than is *E.mauritanica*. I suggest that this may be due to the increased space available for seedling regeneration on these mounds. *E.burmanii* regenerates in open spaces more readily than does *E.mauritanica* and it may thus be taking advantage of the space left by dying *E.mauritanica*.

Pteronia incana is a sensitive indicator of mound disturbance, showing marked drops in abundance on heavily disturbed sites. *P.incana* is the species that best distinguishes lightly disturbed mounds (correlation coeff.=-0.5830; p=0.03). No other species showed such a strong positive association with lightly disturbed mounds. Grazing of young

and adult plants may contribute to this reduction as the species is almost entirely absent from mounds presently grazed by sheep (pers.obs.). *Galenia africana* becomes common on mounds only in these situations (pers.obs.). A reduction in numbers of *P.incana* may therefore be a useful warning sign indicating the onset of overgrazing.

Rhus/Euclea clumps have an interesting distribution as they are common on some mounds and absent from other seemingly suitable mounds. Dispersal and establishment may thus be somewhat random and unreliable. This pattern may be the result of event driven recruitment (see Mentis *et al* 1989). *Rhus incisa* is also found between mounds so that its habitat requirements do not appear to be as exacting as those of *Euclea undulata*, which is confined to mounds.

R.caroli and *P.utile* produce very few seedlings, but this is offset by their well developed ability to produce adventitious roots and thus reproduce and spread vegetatively. This habit seems well suited to their pioneering, mat-forming successional status.

Young plants of *Euphorbia burmanii* and *E.mauritanica* are more common in *R.caroli* mats than in *P.utile* mats. *Pteronia incana* young plants are entirely absent from *P.utile* mats and are very common in *R.caroli* mats. There thus seems to be a strong trend away from using *P.utile* mats as regeneration sites. Although *Euphorbia* spp. seeds were not actually counted within the mats of *R.caroli* and *P.utile* I strongly suspect that there would be no difference in seed number within the different mats. Dispersal is likely to scatter the seeds randomly and there is no reason why *P.utile* patches should not get any incoming seeds. The problem must lie at some later stage in the cycle. Perhaps seed predation (granivory) is greater in *P.utile* patches, although I believe that this is unlikely. Having eliminated both these possibilities, the phenomenon would appear to be connected with allelopathic properties possessed by *P.utile*. Allelopathy is a controversial topic, and the mechanism certainly needs investigating in this example.

The lack of any seedlings under *E.burmanii* contrasts with the presence of numerous young plants of *P.incana* under *E.mauritanica* adults, but it is difficult to explain. The large number of young *P.incana* plants within *R.caroli* mats may be misleading. *P.incana* favours open spaces for seedling establishment (pers.obs.), and a likely scenario may be that these young plants invaded what was then open space, but the faster growing *R.caroli* surrounded the seedlings giving the impression (as gained by a researcher's fleeting study) that *P.incana* had developed within the *R.caroli* mat. This may have also been the situation giving rise to the large number of young *Euphorbia* plants within *R.caroli* mats, although it is likely that this was not the case as *Euphorbia* spp. are fast growing (pers.obs.) and are not likely to be outgrown by *R.caroli*.

The lack of records in the upper portion of Table 4 is largely due to the inability of *Psilocaulon utile* and *Ruschia caroli* to overgrow any other species. These species lie at the base of the proposed competitive hierarchy, as they are the major space-colonising species (Plates 2a and 2c). When the two species interact, the vegetation at the interface tends to die back, preventing one species from overtopping the other. This form of competitive interaction has been recorded for bryozoans growing on rocks in the marine environment (Buss 1986). The alternative is that one or both species expands to into the space occupied by the other, but this was not commonly recorded for *R.caroli* and *P.utile*.

An important point highlighted by Buss (1986) is that overgrowth observations yield only instantaneous data, and any presumption as to the long term dynamics of an interaction based on such information is necessarily speculative. The assessment of cost of engaging in a competitive encounter is not revealed by (most) competitive rankings - reproductive output data are needed for this. In addition, overgrowth need not be harmful. Hence, static observation of competition does not allow assessment of either the eventual outcome or the potential

severity of a particular interaction. We are looking at the phenomena through a very narrow temporal 'window'.

Euphorbia mauritanica is the most vigorous of the common mound species, able to overtop all but *Rhus/Euclea*. It is however, short-lived (pers.obs.), and this means that we must consider the temporal changes in the interaction Although *E.mauritanica* may be overgrowing another species, the sub-canopy species may be able to persist (especially if it is a woody *Pteronia incana)* until the *Euphorbia* dies, leaving a large open space which wil be readily exploited by the once shaded species.

With the help of the data in Table 4 it is possible to arrange the key species in a definite successional sequence. A $<$ sign indicates that the righthand species is able to ovegrow the one on the left, while a $\leqslant$ sign indicates that the two show approximately equal levels of overgrowing each other *i.e.* they appear to be competitive equals. Yeaton *et al* (1977) found that some species in an Arizona community competed with each other, while others did not. Those that did not may be analagous to the competitive equals suggested in the present study. Yeaton *et al* (1977) suggested that root separation was a mechanism which prevented possible interspecific competition, and this may certainly be the case here for *Pteronia incana* (deep roots) and *Euphorbia burmanii* (shallow roots) and *Rhus/Euclea* (deep) and *E.mauritanica* (shallow). The inferred competitive hierarchy for the key species at Worcester is as follows :

Open space $<$ *Psilocaulon utile* $\leqslant$ *R.caroli* $<$ *E.burmanii* $\leqslant$ *Pteronia incana* $<$ *Euphorbia mauritanica* $\leqslant$ *Rhus/Euclea*

The fact that the species can be arranged in a definite, non-random sequence suggests that successional processes are active on mounds. This is an important finding as many previous studies have suggested that there is seldom any predictable succession in arid and semi-arid plant communities (see Mentis *et al* 1989). Disturbance is usually

more frequent on-mound (Milton *et al* -In press; pers.obs.), and I believe that this is the key to understanding the presence/absence of arid-land succession. Most previous studies of arid-land community dynamics have been concerned with off-mound areas (Yeaton *et al* 1977; Mentis *et al* 1989), and it is for this reason that explanations involving stochastic events have assumed a greater importance than have successional explanations. Previous studies have concluded that succession is unimportant in arid-land communities simply because they have not focussed on areas that are subject to frequent disturbance *e.g.* heuweltjies. I therefore predict that successional sequences will be more pronounced on-mound than off-mound, as the disturbance associated with the mounds is what drives the succession. Suitable levels of disturbance are absent off-mound and therefore succession is not clearly visible. To say that succession is unimportant in arid-lands is only correct if one ignores the presence of heuweltjies, and this would be unwise as mounds make up an important structural and functional component of many arid areas in the Cape Province (Lovegrove and Siegfried 1986), and further afield *e.g.*Tanzania (Mielke 1978).

Rhus/Euclea clumps are the woodiest component of the mound flora. This, combined with their ability to grow taller than any other key species, would suggest that they are a suitable (typical) climax vegetation. Plate 2e illustrates an interaction between *Rhus* sp. and *Euphorbia mauritanica* in which the former appears to be overgrowing the latter (which has now reached its maximum possible size and is beginning to die at the centre). This is an example of where a simple advantage of structural height allows one species to dominate.

Exclosures

The young *Euphorbia mauritanica* transplants in the controls were uneaten, possibly because they were already too big and producing latex. The only vulnerable stage may be the seedling stage, and this should be tested by planting seedlings in the plots. The exclosures were only out for three months and this is probably tooshort a period

for changes in the perennial component to become evident. It is however clear that the annual component can be severely reduced by herbivory (Figure 1). It is possible that certain annuals will be eliminated from an area as a result of the adult plants being eaten before they can flower and set seed.

Granivory experiment

Rhabdomys pumilio is apparently equally active on both heavily and lightly disturbed mounds, as equal quantities of seed were removed from both sites. This rodent seems to be almost entirely confined to the heavily vegetated on-mound sites, and it is therefore only in dense vegetation that seed predation is a major consideration (Figure 2). On-mound species must therefore have some strategy to prevent all their seeds being eaten, *e.g.*mast fruiting, directed seed dispersal to favoured sites, spiny seeds. It has been shown that a short handling time is a very important component of seed selection by rodents (G.Kerley -pers.comm.), and I thus predict that seeds of on-mound species should have longer handling times than seeds of off-mound species in order to discourage seed predation by the active rodent population.

Intense granivory on-mounds may be a possible cause of the stable species composition on-mound (*i.e.*there are numerous off-mound species which are never found growing on-mound), as the off-mound species suffer very high seed predation rates on-mound. This could be tested by planting seeds of the relevant species on-mound and monitoring their fate.

CONCLUSIONS

This study demonstrates that small, non-domestic mammals may have a major influence on mound community structure and dynamics. Mammmals as different as small rodents and the aardvark contribute to the

disturbance regime on-mound by eating seeds, defoliating plants, extensive burrowing and creating middens. The disturbance regime can easily vary over time as the various animals migrate or experience population fluctuations. The influence of sheep grazing will add a new dimension to mound dynamics and this would be an interesting study, using the present study as a basis for comparisons. This variation in disturbance is then reflected in the vegetation and floristic structure of the mound community. The vegetation dynamics can in turn be understood in terms of a simple successional sequence, with certain species favouring open, disturbed sites and others favouring dense, undisturbed areas. The discovery of a predictable successional/competitive hierarchy is noteworthy, as much of the present literature suggests that succession is not an important process in arid-land vegetation dynamics (Mentis *et al* 1989). It is proposed that the increased disturbance levels associated with mounds (Milton *et al* -In press; Pers.obs.) are responsible for the visible succession not seen nearly as clearly off-mound.

The role of climate in structuring plant communities is increasingly coming into question as people become concerned with the possible long-term effects of ozone depletion and the greenhouse effect. Reduced rainfall may lead to the inhibition of a successional sequence on mounds as stochastic events become more important. There is some evidence for this : In the dry Tierberg study site *Pteronia pallens* seems to recruit in cohorts (stochastically) on-mound (pers.obs). Recruitment in an unfavourable habitat (such as on-mound, for this species) may be limited to suitable event periods. In addition, there is less evidence of a successional sequence on the drier Tierberg mounds relative to the moister Worcester mounds.

It is difficult to see how a climax mound full of *Rhus/Euclea* will revert to any other stage. Grazing by wild animals is unlikely to have any significant impact on these large bushes ~~to any significant degree~~. A more simple solution may be the presence of pathogens and dense infestations of caterpillars which have been seen to kill large parts of certain bush patches (pers.obs.) A dead *Rhus/Euclea* would leave a large open space

susceptible to invasion by any earlier succesional stage, as their rootsprouts are likely to be outgrown by the other species.

Ruschia caroli and *Psilocaulon utile* are effective space-colonisers that rely both on seed dispersal and vegetative lateral shoots to colonise new areas. It is not known why one species should establish instead of the other, but there is probably an element of chance involved.

Heuweltjies are thus centres of animal and plant activity and may contribute much to the diversity of species and animal/plant interactions in any arid or semi-arid area. Their dynamics may be very different from the dynamics of inter-mound areas and this should be remembered when referring to "arid-land dynamics" in general. The mechanisms and results of the different possible animal/plant interactions are barely understood and will provide stimulating research topics for many years.

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